

Studies in the Helminthocladaceae (Rhodophyta): *Helminthocladia*¹

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DURING RECENT WORK in the field with the algae of Hawaii several interesting red algae have been found. Two of these interesting algae which seem to be members of the Helminthocladaceae are reported here, in the hope that more work with such algae will be encouraged.

The Helminthocladaceae is accepted as being a family, the limits of which would include eight genera that are rather well known and perhaps three genera that are not well known, *Ardissonaea*, *Dorella*, and *Endosira*. *Ardissonaea* was described by J. Agardh (1899: 99) and is treated by Kylin (1956: 127), under the name of *Neoardissonia* Kylin, as a member of the Naccariaceae. *Dorella*, which may be a member of this family, has terminal cortical cells which are not enlarged. According to a personal communication from Dr. H. B. S. Womersley, the type of *Ardissonaea* is a very finely branched alga and *Endosira* appears to be a juvenile of a different order. Kylin (1956: 557) suggests that *Endosira* may be related to *Nemastoma*. Consequently, we shall consider these genera no further in connection with the algae being described below.

Of the eight easily recognizable genera, only *Helminthocladia* possesses lateral carpogonial branches and zygotes (post-fertilization carpogonia) which divide transversely, longitudinally, or obliquely and give rise to a dense gonimoblast from both division products. In addition,

in *Helminthocladia* the terminal vegetative cells in the cortex are strongly enlarged. Kylin (1956: 108) uses this latter as a key characteristic to separate this genus from *Helminthora*. There are other differences between the two genera: In *Helminthora*, for example, only the upper cell of a transversely dividing zygote gives rise to gonimoblast filaments. *Trichogloea* differs from *Helminthocladia* and from other well-known genera in having straight terminal, rather than curved lateral, carpogonial branches and in its calcification. *Dermonema* has long been a relatively unknown genus but is distinct in form, being erect cushions formed of noncalcified closely dichotomous branches, sometimes like *Chnoospora minima* in looks and habitat. Both *Dermonema* and *Cumagloia* (Gardner, 1917: 401) are distinct in having a diffuse gonimoblast ramifying among the cortical filaments near the zygote from which it originated as a few protuberances with no previous division of the zygote. The genus *Liagoropsis* of Yamada (1944) is like *Nemalion* (Desikachary, 1957a), having straight carpogonial branches, but differs in being calcified.

On the basis of various characteristics the algae to be described are judged to be distinct, new species of *Helminthocladia*. They represent the only records of this genus of the Rhodophyta for the Central Pacific Ocean.

Helminthocladia simplex sp. nov.

Figs. 1-18

DESCRIPTIO TYPI: Thalli irregulariter cylindrici, usque ad 9.5 cm. alt., acibus ramisque subsimplicibus saepissime 1 ad 1.5 mm. diam. Rami pauci, irregulariter dispositi. Thalli saepe simplices, qui saepe latiores quam thalli ramosi, raro, autem, plus quam 2 ad 4 mm. diam. Thalli simpliciores forma magis irregulares, clore magis obscuri, statura breviores saepe carpogoniales sunt. Thalli antheridiales ubique vel

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FIG. 1. The type of *Helminthocladia simplex*, a preparation on a herbarium sheet.

plerumque tenuiores, clore nitidiores, altiores, magis ramosi. Thalli textura ubique lubrici mollesque. Frondes multiaxiales, filamentis corticalibus nullo modo inter se adhaerentibus.

The holotype is a preparation of six thalli on one herbarium sheet deposited in the Bernice P. Bishop Museum in Honolulu, Hawaii. These specimens, along with a small *Liagora*, formed a turf on an almost horizontal rock surface just above extreme low tide line. The type material was collected by Jan Newhouse and Henry Keoanui (M. Doty no. 12691) at Kahanahaiki, Waianae, Cahu, Hawaiian Islands ($21^{\circ} 32' N.$, $158^{\circ} 14' W.$), Jan. 2, 1954. Isotypes are being sent to the herbaria of the University of California, University of Michigan, Hopkins Marine Station of Stanford University, Cryptogamic Laboratory of the Paris Museum, University of Adelaide, South Australia, and Hokkaido University at Sapporo, Japan.

During some of the years since the original collection was made by Newhouse and Keoanui, the type locality has been revisited. The sand shifts a great deal throughout the year at this site; sometimes the place is completely covered with sand. Until recently the alga had not been refound, though other members of the Helminthocladaceae were often present in abundance. However, on Apr. 10, 1960, while Doty was accompanied by Newhouse and Ernani Menez, a dense stand of *H. simplex* (M. Doty no. 19135A, Menez no. 201) was found. The thalli were essentially of the same mor-

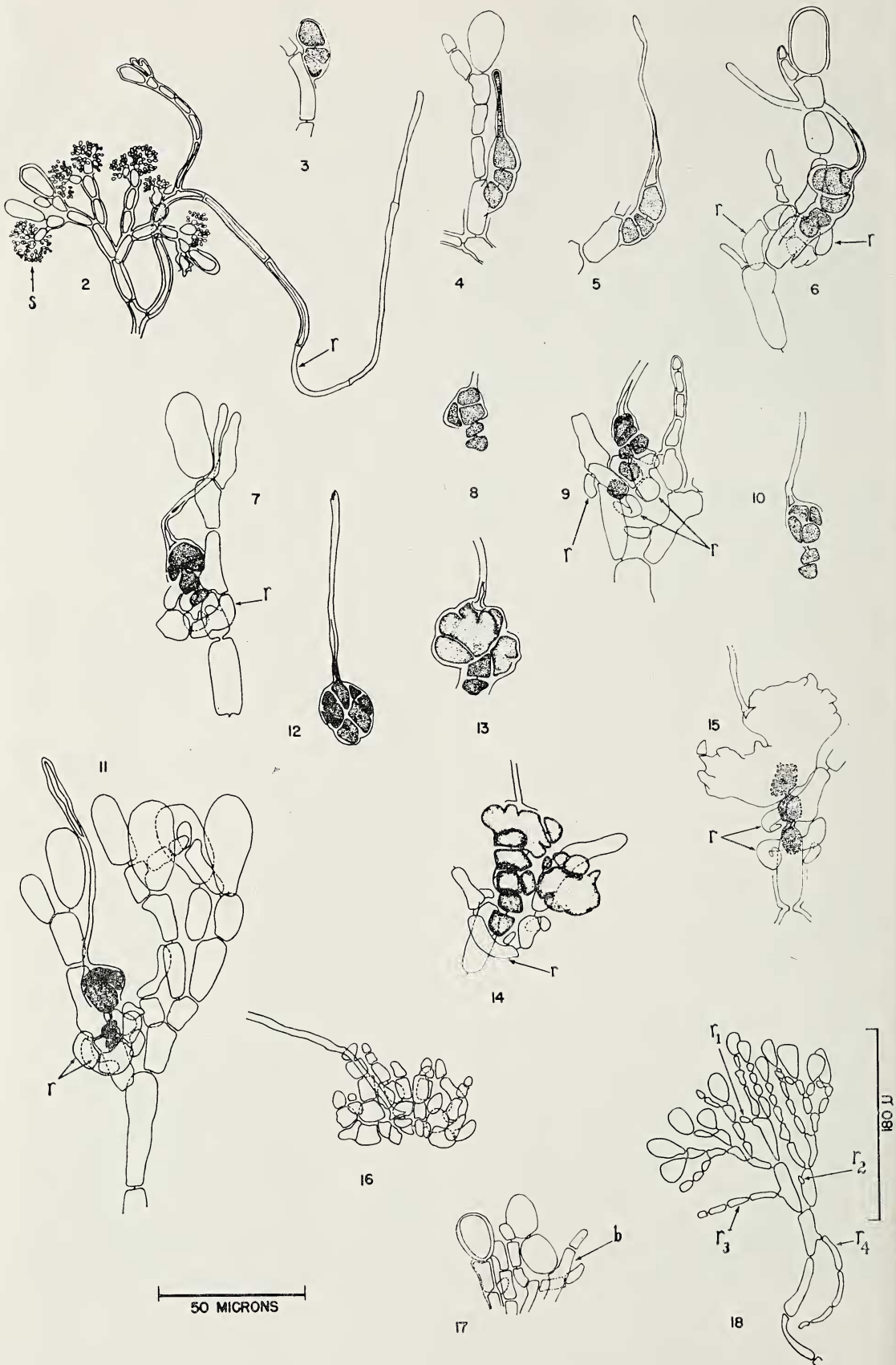
phological form and were collected in the same place under the same conditions as the type. The living material was yellowish brown, with no taste or odor, and hard like a *Gracilaria* rather than soft like a *Trichogloea*. Perhaps a half liter of the species was obtained at this time. In time the algal population dwindled and the sand as well, until by May 8 there was very little of either on the site. The form of the *Helminthocladia simplex* present at this time was still the same as the other collections of this species, or perhaps a bit more eroded.

Thalli (Fig. 1) of irregularly cylindrical branches, up to 9.5 cm. tall, with most of the subsimple axes and branches 1–1.5 mm. in diameter. Branches irregular in arrangement and few. Thalli often simple, and these simple ones, while often of larger diameter than branched thalli, are rarely more than 2–4 mm. in diameter. Often the simpler thalli of more irregular form that are duller in color and shorter in stature are carpogonial. The antheridial thalli are generally more slender, more brightly colored, taller, and more branched. Texture rubbery and pliant throughout. The fronds are multiaxial and the cortical filaments do not adhere to each other in any way.

Our material is dioecious. No evidence of what might be a tetrasporangial generation was seen.

The male thalli produce spermatangia on terminal cortical cells among the vegetative filaments of the surface. The spermatangia are produced on cells (Fig. 2*r*) that are smaller than the adjacent vegetative cells and terminate in dichotomous rows of small cells. These small masses of cells do spread out under the cover glass on a microscope slide as do the terminal fans described for *Helminthocladia* by Martin (1939), but one suspects them of covering the surface area of the vegetative terminal cells they replace; i.e., occurring in round brushlike clusters rather than in two-dimensional fans. More than one spermatium may adhere to a trichogyne; those seen stuck to trichogynes were colorless.

The female apparatus develops laterally from the fourth or fifth cell (Figs. 3, 4, 5) below the enlarged terminal superficial cortical cell.



The terminal cell of the developing carpogonial branch is large at first (Fig. 3). Only three-celled carpogonial branches were seen (Fig. 15 notwithstanding). It often appeared (Figs. 5, 6, 7) that the trichogyne cytoplasm became separated from the zygote cytoplasm; this we accepted as evidence that fertilization had taken place. Few cases were studied where we were certain that only the first division of the zygote had taken place. A number of cases were seen where two (Figs. 6, 7, 8), three (Figs. 9, 10, 11), four, or five divisions (Fig. 12) had taken place. From these it was clear that division of the zygote is usually longitudinal or oblique, as in the case of *H. papenfussii* as illustrated by Martin (1939, figs. 17, 18).

Conspicuous post-fertilization changes were not apparent in the carpogonial branch cells other than in those derived from the carpogonium itself. No placental cell formation was seen. Pit connections within the carpogonial branch (Figs. 13, 14) and to the supporting cell and to the supra-supporting cell were not enlarged, or those between the carpogonial branch cells were only slightly enlarged. The hypogynous carpogonial branch cells in older stages (Figs. 13, 14) were "lighter staining" than during earlier stages. In the six or eight cases in older gonimoblasts studied in this regard (e.g., Fig. 15), the central complex of densely staining cells presumably derived from the carpogonial branch had only, at most, "broadened" pit connections. The contents of the supporting and supra-supporting cell were in some cases darkened and shrunken in diameter in this formalin-fixed material.

As in *H. papenfussii* (Martin, 1939), *Helminthora lindaueri* (Desikachary, 1955: 131), and in *Helminthocladia australis* (Desikachary, 1957b), encircling sterile rhizoid-like filaments (*r* in Figs. 6, 7, 9, 11, 14, 15) after fertilization grow especially around the hypogynous

cells of the carpogonial branch. These were not seen to invade or surround older gonimoblasts of *H. simplex* when these were producing surfaceward-growing filaments. In fact they seemed largely to have disappeared or become lost in our preparations of older stages.

Gonimoblast initials appear from both primary division products of the zygote (Figs. 9–13). The cells of the young gonimoblast (Figs. 10–12) are at first in a dense regular mass which becomes lobed (Figs. 13, 14, 15) in time. In this respect our organism is like other *Helminthocladia* species and unlike other genera in the family.

From the dense indefinitely lobed central gonimoblast mass, sparsely branched rather parallel filaments (Fig. 16) grow towards the surface of the thallus. The gonimoblast filaments are usually unbranched for the terminal three cells. It may well be, though not followed out closely, that the terminal two cells tend to become carposporangia and the bottom (third one) gives rise (Fig. 17b) to a two-celled branch that in turn grows to look like the terminal two cells of the parent filament before they began enlarging into carposporangia. This same third cell may produce another branch. It is interesting to note this sympodial manner of growth here.

In some cases the third cell in the row becomes a carposporangium. In this respect the organism at hand approaches that condition illustrated by Kylin (1930, fig. 2D) for *H. calvadosii*. That is to say, there is nothing like the branching which Papenfuss (1946, fig. 25) illustrates for the homologous structures in *Trichogloea*.

DISCUSSION: The type, MD 12691, is distinguishable from the classical *Helminthocladia budsoni* and *H. calvadosii* (accepted as the type species of the genus as circumscribed by Hamel,

FIGS. 2–18. Reproductive and anatomical features of *Helminthocladia simplex*. 2, Cellular details of a cortical filament system bearing spermatangia (*s*) apically and a rhizoid (*r*) from the assimilatory region. 3–5, Young carpogonial branches (stippled). 6–15, Stages in the development of the gonimoblast with its enveloping rhizoids. Individual cells are indicated by dark stippling; groups of cells are indicated by light stippling; enveloping rhizoids are indicated, and an assimilatory apical cortical cell. 16–17, Branching of the carpospore-producing filaments (*b*). 18, Cellular details of a cortical vegetative filament system showing the strongly dichotomous branching and, from the inner cortical regions, rhizoidal filaments (*r*).

1930), and from all other species known to the authors, in the reproductive structures described for these taxa and on the basis of their being more branched and larger in size. Specimens of *H. calvadosii* from France (University of California Herbarium no. 407401, identified by Kylin) measured 26–36 cm. tall, and in the parts examined lacked any trace of the sterile rhizoid-like filaments characteristic of our species and of *H. papenfussii*. Another specimen (University of California Herbarium no. 218320, labeled by Rosenvinge *H. purpurea*) was up to 60 cm. tall and likewise lacked the peculiar rhizoidal filaments around the hypogynous cells. This latter specimen was the most nearly simple in branching of any *Helminthocladia* examined by us aside from *H. simplex*. In regard to the enveloping rhizoidal filaments our organism is unlike *H. calvadosii* (Kylin, 1930), *H. hudsoni* (Feldmann, 1939) which have no such filaments, and *H. papenfussii* as described by Martin (1939) which has many such filaments. The most striking of these sterile filaments (Figs. 8, 9, 12, 14) arise from the cell above the supporting cell in the vegetative branch, but they are more complex than those Balakrishnan (1955) illustrates for *Lia-gora erecta*.

Martin (1939) ascribes both a fusion cell to *Helminthocladia papenfussii*, derived from the carpogonial branch, and a sterile envelope; these are illustrated in her figures 20 and 21. By the time a gonimoblast is this far developed in this Hawaiian species, there is no indication of either such a fusion cell or such an enveloping basket of sterile branches. The sterile rhizoidal branches develop in *H. simplex* as in some other *Helminthocladia* species where such may be found, primarily from the cell above the supporting cell in the vegetative branch, as Kylin (1938, fig. 1C) illustrates *H. papenfussii*. The first to appear tend strongly to encircle the young gonimoblast but they were not seen in older stages. Desikachary (1956, figs. 25, 29) illustrates a similar situation in *Helminthora lindaueri* from New Zealand.

The material reported and figured as *Helminthocladia australis* by Okamura (1916: 21) and by Segawa (1957: 58, fig. 254) seems to

be similar to ours in habit, except for the larger size and greater degree of branching. However, Narita's (1918) figure of *H. yendoana*, which in that author's opinion includes *H. australis* of Okamura, does not resemble our alga at all. Furthermore, our examination of certain specimens (University of California Herbarium nos. 335335, a female thallus apparently identified by S. Narita; 279932, a female thallus identified by Y. Yamada; and 418162) shows the Japanese material to be different in other details as well. From the materials illustrated and discussed as *H. australis* by Desikachary (1957*b*), our material differs in being far simpler and smaller.

We refer here only briefly to the rhizoids (Fig. 18*r*) which develop from the lower cells of the cortical filament systems. Only rarely was there any indication of such a rhizoidal filament (see *r* in Figs. 2) in the outer part of the cortex that even recalls slightly the rhizoids peculiar to the next species. Figure 18 *r*₁–*r*₄ perhaps illustrates the ontogeny of this rhizoidal type. Note that the cortical cells (Fig. 18) are, in general, characteristic for *Helminthocladia*.

Helminthocladia rhizoidea sp. nov.

Figs. 19–24

DESCRIPTO TYPI: Thallus 9 cm. alt., valde mucosoideus, in partibus inferioribus radiatim ramosus; filamenta corticea usque ad 350 μ long., irregulariter dichotome tritomeve ramosa; cellulae apicales amplificatae, pyriformes, 13–26.5 μ lat., 45 μ long.; rhizoidea multa 4.8–7.2 μ lat., e filamentis corticeis exterioribus producta; gonimoblastus involucre filamentorum e cellulis minoribus quam cellulae corticis vegetativi consistantium, aliter, autem, filamentis assimilativis corticeis propinquis similium, circumdatus; filamenta involucri e cellulis vegetativis infra superque cellulam sustentem producta.

The holotype is a preparation bearing the collection number MDoty 12860. The specimen was collected by Mr. Tetsuo Matsui at Lahaina (156° 41' W., 20° 53' N.), on the island of Maui, Hawaii, and it is deposited in the Bernice P. Bishop Museum, Honolulu, Hawaii.

Thallus (Fig. 19) of cylindrical branches, 9 cm. high, branching radial in the lower portions, the branches 4 mm. in diameter at their bases, gradually tapering to 1–2 mm. in diameter at the tips, strongly mucosoid. The main branches give rise laterally to shorter ones of irregular length between 1 and 3 cm. long. Basal disc 5 mm. in diameter.

Cortical filaments (Fig. 20) up to 350 μ in length, irregularly dichotomous or trichotomous, the lower cells ovoid to cylindrical, the terminal cells inflated and pyriform, 13–26.5 μ wide \times 45 μ long. Short unbranched filaments, usually without the terminal pyriform cells, are commonly borne at the tops of the cortical filaments (Figs. 21*f*, 24*f*). Numerous, sometimes branched rhizoids 7.2–12 μ wide are produced from the medullary filaments. Rhizoids are also produced (Fig. 21*r*) by upper cells of the cortical filaments at first as protuberances 4.8–7.2 μ wide on the lower edge of the cells (Fig. 22*r*), then by elongation cutting off segments (Fig. 23*r*). They are linear, unbranched, and seem to con-

nect neighboring assimilatory branches to each other, whereas those rhizoids produced nearer the axial strand add thickness to the axis. Occasional hairs (Fig. 21*b*) may be formed on the terminal cortical cells.

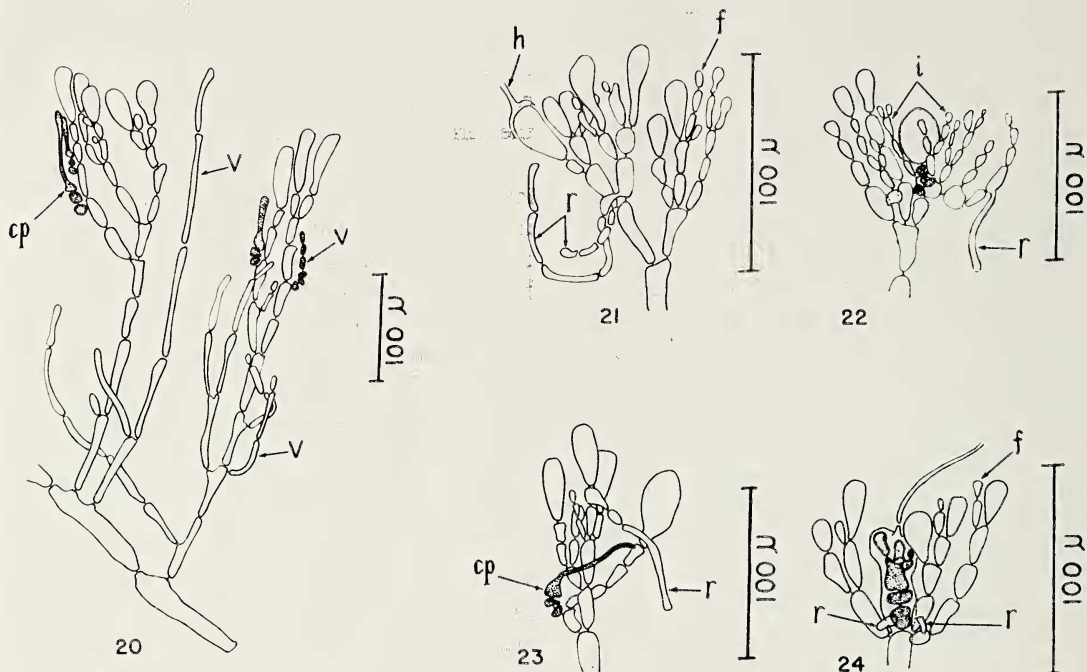
Carpogonial branches 3-celled, curved, mostly lateral as specially formed branches (stippled in Figs. 20, 23) at or near a dichotomy, but occasionally taking the place of a vegetative branch at a dichotomy. If unfertilized, they may develop into cortical filaments (Fig. 20) that are of smaller diameter than the ordinary cortical filaments. The first division of the gonimoblast is longitudinal. Gonimoblast dense, regular in shape (Fig. 22), soon becoming an irregularly shaped dense mass of filaments with only the end cells producing carpospores.

A few sterile filaments are produced from the vegetative cells above the supporting cell (Fig. 24) or from those subtending the supporting cell (Fig. 22). They loosely bracket and overtop the gonimoblast (Fig. 22*i*), together with the vegetative filaments deflected by the growth of the cystocarp. No fusion cell is formed.



FIG. 19. The type of *Helminthocladia rhizoidea*, a single specimen preserved on a herbarium sheet.

DISCUSSION: In its vegetative appearance (Fig. 19), *H. rhizoidea* is similar to certain other species of *Helminthocladia*, such as some forms of *H. australis* (Desikachary, 1957*b*, pl. 16, fig. 3). It is a strikingly different alga from *H. simplex*, described above (Fig. 1), which it does not resemble in either external or internal structure. However it is generally similar in external appearance to other well-described species of *Helminthocladia*; i.e., *H. calvadosii* (Kylin, 1930), *H. papenfussii* (Martin, 1939), and *H. australis* (Levring, 1953; Desikachary, 1957*b*). *H. rhizoidea* differs from these because of the production of decumbent rhizoids (*r* in Figs. 21–23) from the basal ends of the vegetative cells, which constitute the assimilatory filaments. While this fact in itself may not be of first importance, it does clearly separate this species from other species of *Helminthocladia*. Rhizoidal structures do appear nearer the medulla in *H. simplex* (Fig. 2) and in the *Helminthocladia* studied by Desikachary (1957*b*: 442, fig. 5), but these seem to have a different origin (see Fig. 18). It would seem that vegetative



FIGS. 20-24. Cellular reproductive and vegetative peculiarities of *Helminthocladia rhizoidea*. 20, A cortical heterofilamentous system, wherein some branches are of slender long cells (*v*) and some terminated by "normal" obpyriform cells, normal (e.g., *cp*) and seemingly abnormal carpopogonial branches. 21, Cellular details of a cortical vegetative system illustrating a hair base (*b*), slender cortical filaments (*f*), and two of the rhizoids (*r*) which characteristically issue from the assimilatory region. 22, Origin of a rhizoid (*r*) from an assimilatory cortical filament, a well-developed gonimoblast (lightly stippled) with three hypogynous cells (darkly stippled) and several small-celled involucre filaments (*i*). 23, One of the rhizoids (*r*) peculiar to this species and well-formed carpopogonial branch (*cp*). 24, A young gonimoblast with two one-celled encircling rhizoids (*r*) developed from supra-supporting cells, and a slender cortical filament (*f*).

characters of this kind are necessary aids to distinguishing the ever growing number of species in this genus.

The sterile filaments surrounding the cystocarp of *H. rhizoidea* (Fig. 22*i*) appear to resemble closely those in *H. papenfussii* as illustrated by Martin (1939), although the derivation of the sterile filaments may not be the same in both species. Martin states that the sterile filaments arise from the vegetative cell above the supporting cell in *H. papenfussii*. This is true also in *H. australis* (Desikachary, 1957*b*) where, however, they may also arise from the cell below the supporting cell. The derivation in *H. rhizoidea* also may be from above or below the supporting cell.

The possession of a loose basket of sterile filaments around the gonimoblast in *H. rhizoidea* seems to furnish a further characteristic for distinguishing this species from *H. simplex*. Only the initial few cells of the involucre are illustrated in Figures 22 and 24 for *H. rhizoidea*, while perhaps the ultimate in development of rhizoids is given in Figures 6, 7, 9, 11, 14, 15 for *H. simplex*.

Most species of *Helminthocladia* appear to have fairly regularly dichotomous assimilatory filaments; see the illustrations of *H. calvadosii* (Kylin, 1930), *H. hudsoni* (Feldmann, 1939), *H. australis* (Desikachary, 1957*b*), and those of *H. simplex*, especially Fig. 18 in this paper. In this respect *H. papenfussii* and the present

species are similar to each other in that the branches near the tops of the filaments are often trichotomous. The ultimate cells of the cortical filaments are more crowded, therefore, than those of most other species. Often in this genus where the cortical filaments are not dichotomous the production of carpogonial branches or rhizoidal branches (of the type illustrated in Fig. 18) seems to have been involved. Either normal carpogonial branches may have appeared (Figs. 20*cp*, 23*cp*), or abortive carpogonial branches may have become reorganized (Fig. 20*v*), possibly into vegetative branches.

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